The Long-Term Consequences of Deer Browse in Temperate and Boreal Forests

Honors Thesis

Samuel Powers Reed

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Thesis Committee:

Dr. Peter S. Curtis (Research Adviser)

Dr. Roger A. Williams (Academic Adviser)

Dr. Lauren M. Pintor

Abstract:

White-tailed deer (*Odocoileus virginianus*) overabundance has sparked dramatic changes in forests throughout North America. In Pennsylvania's Allegheny National Forest and Quebec's Anticosti Island, I investigated how deer have altered canopy structural complexity, species diversity, and carbon stocks across a controlled density gradient and a chronosequence of increasing disturbance, respectively. To measure canopy complexity, I used a Portable Canopy LiDAR (PCL) system, which records the three-dimensional arrangement of leaves and stems within a canopy using an upward-facing infrared laser. In Pennsylvania we predicted that treatment effects on forest composition and structure would support the intermediate disturbance hypothesis and that stands experiencing moderate levels of deer browse during the early stages of regeneration would show increases in canopy complexity, carbon sequestration, and diversity. In Anticosti we predicted a significant increase in canopy complexity and carbon storage between deer preferred and non-preferred stands and as stand age increased.

Introduction:

Over the last century, white-tailed deer populations (*Odocoileus virginianus*) have rapidly increased throughout the eastern portion of America. The increase in population size and browse intensity has altered many forest's regenerative capacity and their resulting structure (Cote et al. 2004). Changes in structure and biodiversity alters a forest's ecological functions, such as carbon sequestration, water filtration, or wildlife habitat (Bengtesson et al. 2000). As deer populations continue to be stressors on forest ecosystems, managers and the public must adapt to a changing landscape or find a solution to the high population levels.

As deer change forest communities, they likely alter canopy structural complexity (CSC), the three-dimensional arrangement of leaves and branches within a canopy. CSC has been implicated as an important factor in aging forests' ability to maintain functionality, such as carbon storage or wildlife habitat (Hardiman et al. 2013b; Ishii et al. 2004, Jung et al. 2012). As forests age and experience moderate abiotic disturbances, their canopies may become more complex. Net primary productivity (NPP), the rate that plants take in carbon and grow, appears to increase as a function of structural complexity, as light and nitrogen are used more efficiently (Hardiman et al. 2013a). However, the impact of large or chronic biotic disturbances on canopy structure have not been analyzed.

In both Pennsylvania's Allegheny Plateau and Quebec's Anticosti Island, I analyzed how deer shifted forest types through selective browsing. Both sites have had high deer populations throughout the 20th and 21st century (Leopold et al. 1947; Potvin et al. 2003) and are extensively clearcut for timber. Clearcuts allow deer to browse on regenerating seedlings and alter canopy structure, especially when other food is scarce during the winter months.

Allegheny Plateau:

There has been an overabundance of deer on the Allegheny Plateau since the early 1920's, as hunting regulations and deer protections were established (Leopold et al. 1947). Average deer density reached 11.6-19.2 deer/km^2 in the 1930s, dropped to ~5.4 deer/km^2 in the 1940s due to severe winters, and rose to 15.6-22.6 deer/km^2 by the 1970s before the initiation of this study (Horsley, 2003). Between 1950 and 1970 a renewal in timber production increased deer densities and allowed for overabundance (Horsley, 2003).

Within the region, most herbivory studies focused on excluding deer from plots, with some exclosures in use for over 60 years (Goetsch et al. 2011). Although exclosures provide valuable information, there is little control over the ambient environment's deer population or browse intensity outside of the fencing, making it difficult to justify that the vegetative regeneration is generalizeable. In contrast, deer enclosures allow for control over population size and the resulting browse intensity.

In 1979 and 1980, the U.S. Forest Service established four 65 ha deer enclosures throughout the Allegheny Plateau that were in use for 10 years (Tilghman, 1989). The four 65 ha deer enclosures contained subenclosures of 4, 8, 15, and 25 deer/km^2, which represent historical deer densities from the late 19th century to present time. To model a 100-year heavy management scenario, each density was treated with three different cutting schemes, clear cut, cut to 60% residual relative density, and uncut (Tilghman et al, 1989). After 30 years, each subenclosure has maintained the residual effects of long-term browsing, such as browse-tolerant species dominating high deer density treatments (Nuttle et al. 2011) (Figure 2).

In this study we investigated how deer have altered canopy structural complexity, biomass, and species diversity within each density treatment's former clear cut (n=16). Our null hypothesis was that deer have no significant effect on the three aforementioned variables. In

contrast, our alternative hypothesis was that each of variable would peak at intermediate deer browse intensity, in accordance with the intermediate disturbance hypothesis (IDH) (Connell, 1978). These results would provide more support for the IDH and justifies further research on how deer have altered forest's canopy structural complexity and function throughout the U.S.

Anticosti Island:

During the late 19th century a herd of nearly 200 deer were imported to Anticosti Island, Quebec by chocolatier Henri Menier. Anticosti Island serves as a 7,493 km^2 enclosure where game are unable to migrate due to the island's distance from the mainland. Therefore, the deer have proliferated throughout the island and have rapidly altered the forest landscape. Balsam fir stands were formerly the dominant forest type, but have shifted to white spruce with intense herbivory (Potvin et al, 2003). Remaining balsam fir stands are expected to be eliminated within 30 to 40 years (Potvin et al. 2003).

In this study, we used a chronosequence of disturbance to investigate how deer have influenced canopy structure, biomass, and species diversity over the last 120 years on Anticosti Island. We investigated how these variables change along a chronosequence of 30, 50, 70, 90, and 120 year old plots within pure white spruce or balsam fir stands to represent the former and current dominant forest types (n=14) (Figure 2).

Our null hypothesis is that both time and deer browse will have no effect on the structural complexity and biomass of both white spruce and balsam fir. Our alternative hypothesis is that there will be an increase in structural complexity and biomass over time and a significant difference between the structural complexities of both balsam fir and white spruce stands at the 70 and 90 year age class. We could only compare white spruce and balsam fir at 70 and 90 year

old plots because these are the only age classes where both exist, since deer had not spread across the entire island until after 70 years. We predicted that both rugosity and biomass would have a positive correlation with time due to both variables being dependent on stand height and a well-developed canopy. We predicted a difference in structural complexity between balsam fir and white spruce due to a predicted lack of a mid-story within balsam fir stands, as intense browse pressure removed regenerating balsam fir seedlings. These results would indicate that deer are having a significant effect on the canopy structural complexity of Anticosti's forests and that they could be influencing the carbon sequestering ability of the landscape.

Literature Review:

Forest Disturbance:

Although "ecological disturbance" often has a negative connotation, both abiotic and biotic disturbances are crucial to the function and structure of forests worldwide. Within the United States, forest dynamics are driven by herbivory, fire, drought, introduced species, insect outbreaks, hurricanes, or ice storms, with each of these disturbance regimes being altered by climate change and anthropogenic forcings (Dale et al. 2001). The intensity of these disturbances can have extensive effects on the development and function of forest ecosystems over both brief and extended time scales.

One of ecological disturbance's influences over long time periods is succession, or the changes in a community when a perturbation occurs (Connell, 1977). Disturbance facilitates forest succession by opening gaps within the canopy, which releases tree species residing in the understory. Over time, frequent perturbations create a developed forest with multiple age classes and higher species diversity. Forests altered by disturbances can then have increased or decreased function, or the "work" that an ecosystem does, such as cycling nutrients or

maintaining wildlife habitat. For example, fire drives forest dynamics throughout most of North America through seedling regeneration, nutrient cycling, and improved wildlife habitat (Abrams et al. 1992; Russell et al. 2009). These benefits to forests are then conferred in different ways through other disturbances.

In addition, disturbance intensity is intimately tied to ecosystem stability, specifically ecological resilience and resistance. Resilience is defined as the rate that an ecosystem returns to a pre-disturbance functional state, but this rate is directly proportional to the intensity of ecosystem disturbance (Attiwill, 1994). Resistance is an ecosystem's "inertia," or the system's ability to absorb disturbance without large deviations from the current functional state (Attiwill, 1994). These measures of stability are believed to be directly proportional to the level of diversity within an ecosystem, known as the diversity-stability hypothesis (MacArthur, 1955; Tilman and Downing, 1994). Nevertheless, this hypothesis appears to be largely dependent on controlled experiments, where the community assemblages are random and only one trophic level is analyzed (Hooper et al. 2005). In addition, ecosystem function within many diversity-resilience studies is characterized by biomass production within grasslands (Tilman et al. 1994, 2001; Hector et al. 1999) while many other equally important functions and ecosystems remain unaccounted for.

The diversity-resilience/resistance hypothesis lacks an incorporation of ecosystem stochasticity, as a wide variety of top-down and bottom-up disturbances are not considered. Forest ecosystems are dynamic in that they can and will respond in many ways to the wide variety of disturbances that affect them. To account for this, the intermediate disturbance hypothesis (IDH) focuses on varying disturbance frequency and intensity, predicting that biodiversity and function will peak at intermediate levels of disturbance (Connell, 1978). The

mechanism behind IDH is that mid-frequent disturbances provide time for new species to establish between perturbation bouts, while eliminating competitive exclusion by reducing the amount of species that could dominant a landscape (Connell, 1978). This hypothesis depends on a non-equilibrium state within a community and can be applied to a multitude of disturbances.

Most studies only consider IDH through the lens of species diversity, while there are other ecological indicators that the hypothesis can be applied to. Fahey et al. (2015) found that moderate wind disturbance improved canopy structural complexity and potentially carbon sequestration. In addition, Biswas and Mallik (2010) found that functional traits such as productivity and disturbance tolerance increased with moderate disturbance. Nevertheless, IDH is highly contested on the grounds that fewer than 20% of studies have found the predicted peak in diversity or function at moderate disturbance and that there are logical inconsistencies within the hypothesis (Fox, 2013).

Materials and Methods:

Sampling:

Between both Anticosti and Allegheny, we established 3, 30 x 5 m belt transects in each plot and recorded canopy complexity, species composition, and diameter at breast height (DBH) for all trees > 5 cm DBH. Canopy complexity, or rugosity, was measured using the ground-based portable canopy LiDAR and metrics of complexity were calculated following the methods of Hardiman et al. (2011). Transect length was roughly double the height of the canopy and transect width captured most branches hanging above the LiDAR.

Portable Canopy LiDAR:

Canopy structural complexity was measured using the ground-based portable canopy LiDAR system (PCL; Parker et al. 2004a). The PCL measures the arrangement of leaves and stems within a canopy using an upward-facing infrared laser at 100 Hz along a transect. Utilizing a REIGL rangefinder and LaserWin software we recorded 7500-8500 laser returns across each transect to collect a representative and consistent sample. These returns were then processed in MatLab, which produced key structural complexity metrics, such as rugosity, porosity, and canopy height (Table 1). In addition, we produced hit grids to illustrate the density of returns across each transect in 1 m x 1 m bins that extend in both the horizontal and vertical directions (Figure 1).

Allegheny Plateau

Study Site:

This experiment took place on the Allegheny Plateau in coordination with the U.S. Forest Service. We used four sites in north-western (Fool's Creek, Deadman's Corners) and north-central (Gameland 30, Wildwood Tower) Pennsylvania on the unglaciated section of the Appalachian Plateau (Horsley et al. 2003) (Table 2). The landscape is composed of contiguous forest with interspersed agricultural and natural gas extraction land uses. Precipitation ranges from 1020 to 1070 mm per year and average temperature ranges from 8 to 9 °C (McNab and Avers, 1994). The soils are highly acidic, with the dominant soil orders being alfisols, entisols, inceptisols, and ultisols made from parent materials of sandstone, siltstone, and shale (McNab and Avers, 1994; Horsley et al. 2003). Two sites, Fool's Creek and Deadman's Corners, were located within the Allegheny National Forest, one within State Gamelands 30, and one (Wildwood Tower) on land belonging to the National Gas Fuel Company. All sites were

previously composed of 60-70 year old stands of black cherry, red maple, and sugar maple (Tilghman, 1989).

Deer Enclosure:

Within each site, a 65 ha deer enclosure with 2.5 m high fencing was assembled. Each enclosure experimentally manipulated deer populations at different densities of 4, 8, 15, and 25 deer/km^2 for 10 years (Tilghman, 1989; Horsley et al. 2003; Nuttle et al, 2011). Two enclosures were established in 1979 and the other two in 1980. Each density was treated with three different cutting schemes (clear cut, cut to 60% residual relative density, and uncut). There have never been any measurements of canopy structural complexity within these plots.

Transect and Plot Selection:

We measured a total of 16 plots (n=16). Within each plot, the first transect was randomly established by selecting a GPS point in the plot's center prior to entering. From this central point, two other parallel transects were established 30 m away from the original. We only collected metrics of structural complexity within each subenclosure's clear-cut treatment.

Statistical Tests:

To calculate biomass I used Jenkins et al. (2003) allometric equations to determine the biomass per species within each plot from the DBH measurements. From these calculations we used RStudio's vegan package to calculate species richness, evenness, and Shannon diversity for each plot. From these data I used linear regressions to determine how biomass, canopy structural complexity, and Shannon diversity change with increasing deer browse. In addition, I used One Way ANOVAs to find an overall effect of deer density and Tukey's t-test to compare the effects

of each of the density treatments within the plots. SigmaPlot was the primary statistical software used to calculate these metrics.

Anticosti Island:

Study Site:

This experiment occurred on Anticosti Island (7943 km^2) in the Gulf of St. Lawrence, Quebec (49°50'19.000"N, 64°17'36.000"W). The climate on the island is maritime and average temperatures are -13.6 C in January and 14.8 C in July (Potvin, 2003). The forests on Anticosti are within the boreal zone and belong to the eastern balsam fir-white birch climactic region (Saucier et al. 2003).

From 1896 to 1897 nearly 220 deer were released on the island, with no large predators to suppress the population (Tremblay et al. 2006). Their population peaked within 30 years and has remained consistent at 20 deer/km^2 over the last 130 years (Potvin and Breton, 2005). Intense browse preference for balsam fir has led to its lower regenerative ability and increased white spruce populations (Potvin et al. 2003). Since deer are unable to leave or enter Anticosti, the island serves as a natural enclosure and provides insight to the effects of deer on boreal systems.

Plot Selection:

On Anticosti Island we measured 16 plots. Each age class contained two replicates and each was at least 10 km away from their respective replicate. Within each plot, the first transect was randomly established by selecting a GPS point in the plot's center prior to entering. From this central point, two other parallel transects were established 30 m away from the original. Finally, all stands were similar density, as designated by the natural resource group on the island. This density was the most prevalent on the island and is the most representative.

Statistical Test:

I calculated biomass using the fir and spruce allometric equations provided by Jenkins et al. (2003). I then analyzed changes in white spruce rugosity and biomass over time with linear and quadratic regressions to find an overall effect of age. SigmaPlot was the primary statistical software used to calculate these metrics.

Results:

Allegheny Plateau:

My findings indicate a significant increase in canopy structural complexity in the 15 deer/km^2 treatment, as average rugosity increased from roughly 6.58 m (8 deer/km^2) to 10.15 m (15 deer/km^2) ($p<0.05$; Figure 2; Table 4; Table 5). Between all other comparisons of structural complexity and deer density, there were no statistically significant differences between other treatments (Appendix; Table A)

Biomass and diversity had more variable responses to deer density than canopy structural complexity. There was a significant decrease in biomass with increasing deer density, especially from 4 and 15 deer/km^2 to 25 deer/km^2 ($r^2=0.294$; $p<0.001$; Figure 3; Table 6; Table 7). Biomass dropped significantly from the 4 and 15 deer/km^2 treatments to the 8 deer/km^2 treatments ($p=0.001$, $p=0.002$; Table 6; Table 7) while there was no substantial difference in biomass from the 8 and 25 deer/km^2 treatments ($p>0.05$). Shannon Diversity also decreased significantly with increasing deer density, but there were no significant differences between each deer density treatment ($r^2=0.199$; $p<0.0001$; Figure 4; Table 8; Table 9).

Anticosti Island:

On Anticosti, white spruce stand rugosity increased significantly as time passed (r^2=0.791; p<0.0031; Figure 5; Table 10). Following 70 years, there is no noticeable change in rugosity and the curve stabilizes. With regard to balsam fir stands, there are no significant differences in rugosity between the 70, 90, and 120 year age classes and no differences between balsam fir and white spruce rugosity at the 70 and 90 year age classes (p>0.05).

For all four white spruce age classes, biomass increases regularly until the 90 year age class, after which it decreases (r^2 = 0.777; p < 0.05; Figure 6; Table 11). The pattern that emerges is hyperbolic and peaks at the 70 year age class. In addition, there is a strong relationship between biomass and rugosity, wherein rugosity increases with white spruce biomass until the 70 year age class (r^2=0.769; p=0.0216; Figure 7; Table 12). In contrast, there was no pattern in balsam fir biomass from 70 to 120 years old.

Discussion:

Allegheny Plateau:

The increase in rugosity from 8 deer/km^2 to 15 deer/km^2 was originally believed to be an intermediate disturbance effect (Figure 3), but there is no significant increase in species diversity at moderate deer browse intensity (Figure 4), as would be predicted by the IDH. An alternative explanation is that the significant increase in biomass from 8 deer/km^2 to 15 deer/km^2 (p=0.002; Table 4) caused an increase in structural complexity. This increase in structural complexity and biomass may have been due to natural pin cherry mortality, since this species has a 30-40 year lifespan (Burns and Honkala, 1990) and was abundant in the 8 deer/km^2 treatment. There was more pin cherry located within the 8 deer/km^2 treatment, due to competition from black cherry stump sprouts within the 4 deer/km^2 treatments and intense browse preference in the 15 deer/km^2

treatment (Ristau and Horsley, 1999; Tilghman, 1989). As pin cherry died within the 8 deer/km^2 treatment, there were likely increased canopy gaps and less living material within each plot, decreasing both rugosity and biomass (Table 3; Table 7). These data indicate that IDH may not explain the changes in structural complexity and that our results could be due to tree mortality and new gap formation within the 8 deer/km^2 treatment. In addition, these results may indicate that rugosity is the most precise measure of structural complexity, as it was the only PCL metric that recorded changes within the canopy.

Further, if the biomass at the 8 deer/km^2 treatment decreased recently due to pin cherry mortality, it is possible that the biomass at this treatment is similar to that of 4 and 15 deer/km^2. If this is the case, the sampled forests may have reached a threshold of deer browse disturbance at the 15 deer/km^2 treatment, past which ecosystem function rapidly declines ($p<0.001$; Figure 3). Similar non-linear responses have been observed in other forests, wherein there were abrupt declines in ANPP when basal area loss was above either 61% or 66% (Stuart-Haentjens et al. 2015).

These results do not support my original hypothesis of the intermediate disturbance effect influencing canopy structural complexity, biomass, or biodiversity; therefore, we accept the null hypothesis. In contrast, we found that rugosity is likely the best indicator of structural complexity in light of deer browse and that intense deer browse may lead to a decline in biomass once a certain intensity threshold is reached. These results are relevant due to the high abundance of deer throughout the eastern United States and the lack of understanding of how ungulates alter ecosystem function and health. We believe these data could inform both land managers and citizens as to the proper deer stocking level within an ecosystem in order to maximize function, health, and recreation.

Anticosti Island:

The research on Anticosti Island was entirely experimental, in that it was the first time the PCL had been used within a boreal ecosystem. I found an increase in white spruce structural complexity with an increase in age from 30 to 70 years ($p<0.1$; Figure 5). In contrast, there were no discernable changes in structural complexity for balsam fir over time or differences in structural complexity between balsam fir and white spruce in the 70 and 90 year age classes. Therefore, I can partially reject the null hypothesis and conclude that white spruce forests increase in rugosity over time.

The pattern of white spruce stand rugosity over a chronosequence is similar to the relationship Hardiman et al. (2013b) found in northern lower Michigan, where canopy rugosity increases with forest age. This similarity indicates that the PCL can be used within boreal forests, even though rugosity values are low in comparison to deciduous forests. In addition, rugosity values may serve as an accurate predictor of biomass and carbon sequestration across boreal landscapes. These results illustrate the need to better understand boreal canopies and how their arrangement can influence the amount of carbon absorbed by a system.

Conclusions:

Over the last 100 years, Allegheny and Anticosti's intense deer herbivory has shifted the dominant forest species and caused significant deviations in canopy structural complexity and biomass. Within Allegheny, our results indicate that there may be a threshold of disturbance for northern hardwood forests – even after 30 years. This helps to inform what the ideal stocking capacity could be within the region and contributes to our understanding of tipping points within ecosystems. In Anticosti, the rise in canopy structural complexity and biomass indicates that the PCL may be a useful tool in boreal systems and could serve as a predictor of carbon

sequestration or wildlife habitat. Although no direct comparisons could be made between Allegheny and Anticosti, deer browse has significantly impacted these large landscapes and those living on them. These understudied, widespread, and long-term consequences of herbivory indicate that we have an unsatisfactory understanding of how deer influence eastern forest's functional and adaptive capacity in light of increasing disturbance through climactic and anthropogenic forcings.

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Tables:

Term	Definition
Rugosity	The three-dimensional arrangement of leaves and stems within the canopy
Height	Variability of mean return height
Mode	Variability of mean return height
ModeEl	Mean height of maximum return density
MeanHeight	Mean return height
MeanStd	Mean variability of return height
MeanLAI	Leaf Area Index (LAI) calculated from return
MeanTopel_CPAll	Mean maximum height
Top_rug	Variability of outer canopy surface height
Porosity	Ratio of bins with no returns to total number of bins

Table 1: A list of metrics generated by the Portable Canopy LiDAR. Within both the Allegheny Plateau and Anticosti Island, rugosity served as the most descriptive metric, while other descriptors of canopy structure served to be less useful.

Site	Abbreviation
Deadman's Corners	DMC
Wildwood Tower	WWT
Gamelands 30	GL
Fool's Creek	FC

Table 2: A list of the 4 replicate deer enclosure sites and their abbreviations. Each 65 ha enclosure was subdivided into 4 deer densities of 4, 8, 15, and 25 deer/km^2 and were in use from 1979/1980 until 1990.

	Allegheny Plateau	Anticosti Island
Plots	n = 16	n = 14
Treatments	4, 8, 15, 25 Deer/Km^2	30, 50, 70, 90, 120 Year Age Class
Selection	Haphazard	Haphazard
Transects/Plot	3	3
Transect Size	3 x 30 m	3 x 30 m
Trees Recorded	>5 cm	>5 cm
Deer Preferred	Pin Cherry	Balsam Fir
Deer Avoided	Black Cherry	White Spruce

Table 3: Between Allegheny and Anticosti, deer density and age class were the independent variables while the resulting dominant trees, canopy structural complexity, and biomass are the dependent variables. In Allegheny deer have shifted the species composition from pin cherry to black cherry and in Anticosti from balsam fir to white spruce. The number of transects per plot, transect size, and minimum DBH were consistent between both study sites.

Rugosity	**Diff of Means**	**t**	**P**
15 vs. 8 Deer/Km^2	0.18	3.55	0.024
15 vs. 25 Deer/Km^2	0.12	2.35	0.17
15 vs. 4 Deer/Km^2	0.095	1.86	0.31
4 vs. 8 Deer/Km^2	0.087	1.68	0.31
25 vs. 8 Deer/Km^2	0.061	1.20	0.44
4 vs. 25 Deer/Km^2	0.025	0.49	0.63

Table 4: Comparison of rugosity within each deer density treatment (One Way ANOVA; Tukey's t-test), wherein there were only significant deviations in canopy rugosity between 15 and 8 deer/km^2.

Rugosity (m)	DMC	WWT	GL	FC
4 Deer/Km^2	6.63	8.54	8.83	8.27
8 Deer/Km^2	6.51	7.23	5.89	6.73
15 Deer/Km^2	12.1	8.26	12.0	8.35
25 Deer/Km^2	6.50	6.41	7.94	9.92

Table 5: PCL-recorded canopy rugosity for each plot in order of ascending deer density treatment, with the minimum value in 8 deer/km^2 and the maximum value in 15 deer/km^2.

Biomass (kg)	Diff of Means	t	p
4 vs. 25 Deer/Km^2	2520	6.31	<0.001
15 vs. 25 Deer/Km^2	2270	5.69	<0.001
4 vs. 8 Deer/Km^2	2010	5.04	0.001
15 vs. 8 Deer/Km^2	1770	4.42	0.002
8 vs. 25 Deer/Km^2	505	1.27	0.41
4 vs. 15 Deer/Km^2	247	0.62	0.55

Table 6: Comparison of biomass within each deer density treatment (One Way ANOVA; Tukey's t-test). There were no differences in biomass within two density groups ($p>0.05$; 8 and 25 deer/km^2; 4 and 15 deer/km^2), but between these two density groups there was significantly higher biomass in 4 and 15 deer/km^2 in comparison to 8 and 25 deer/km^2 ($p<0.005$)

R	Rsqr	Adj Rsqr	Standard Error of Estimate
0.543	0.294	0.244	1070
	Std. Error	**t**	**p**
y0	513	14.6	<0.0001
a	33.6	-2.42	0.0299

Table 7: Linear regression indicating the relationship between biomass and deer density, wherein there is a significant downward trend in biomass as deer densities increase ($r^2 = 0.244$; $p<0.0001$)

Biomass (kg)	DMC	WWT	GL	FC
4 Deer/km2	8349	7451	8106	6495
8 Deer/km2	5408	6290	5445	5212
15 Deer/km2	7649	7393	7617	6755
25 Deer/km2	5557	4512	5091	5174

Table 8: Recorded biomass for each plot in order of ascending deer density treatment, with the minimum value in 25 deer/km^2 and the maximum in 4 deer/km^2.

R	Rsqr	Adj Rsqr	Standard Error of Estimate
0.446	0.199	0.142	0.346

	Std. Error	t	p
y0	0.165	8.73	<0.0001
a	0.0109	-1.86	0.0831

Table 9: Linear regression illustrating the relationship between Shannon Diversity and deer density, where there was a weak negative correlation between Shannon Diversity and deer density ($r^2 = 0.199$; $p < 0.0001$). High variance at 15 and 25 deer/km^2 likely reduced the significant downward trend.

R	Rsqr	Adj Rsqr	Standard Error of Estimate
0.889	0.791	0.756	0.663
	Std. Error	**t**	**p**
y0	0.671	-0.647	0.542
a	0.0105	4.76	0.0031

Table 10: Quadratic regression illustrating the relationship between rugosity and white spruce age class, wherein there was a strong positive increase in rugosity as white spruce age class increase ($r^2 = 0.791$; $p < 0.0031$).

R	Rsqr	Adj Rsqr	Standard Error of Estimate
0.882	0.777	0.688	2420
	Std. Error	**t**	**p**
y0	7070	-2.72	0.04
a	259	4.14	0.01
b	2.14	-4.01	0.01

Table 11: Quadratic regression indicating that biomass significantly peaks at the 70 year age class and then decreases towards the 90 year age class ($r^2 = 0.777$; $p < 0.05$).

R	Rsqr	Adj Rsqr	Standard Error of Estimate
0.877	0.770	0.712	0.744
	Std. Error	**t**	**p**
y0	0.856	-0.817	0.460
a	7.85E-05	3.66	0.0216

Table 12: Linear regression output for the relationship between rugosity and white spruce biomass at 30, 50, and 90 year age classes, where there is a strong positive relationship between rugosity and white spruce biomass ($r^2 = 0.77$; $p < 0.0216$).

Figures:

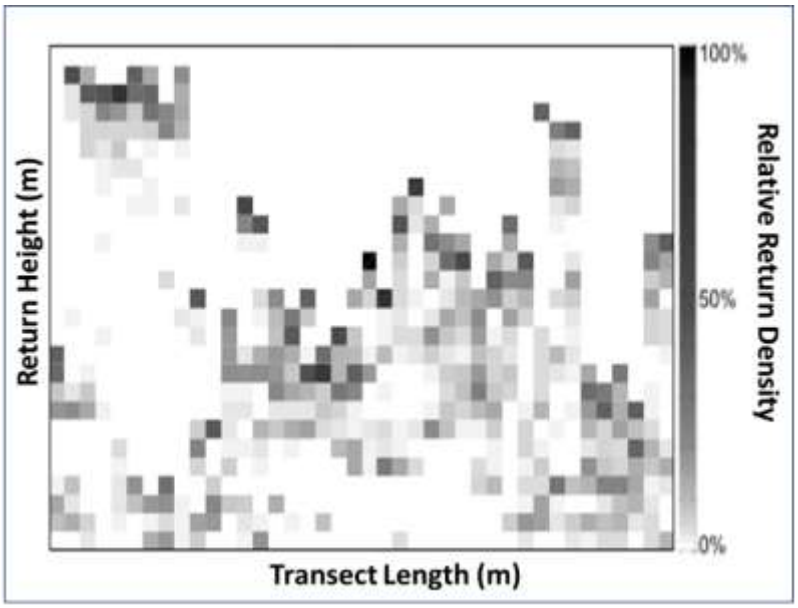

Figure 1: Hit grid for a high rugosity transect, wherein darker shading indicates a higher amount of PCL returns. Rugosity is then calculated using $\sigma(\sigma[VAI]_z)_x$.

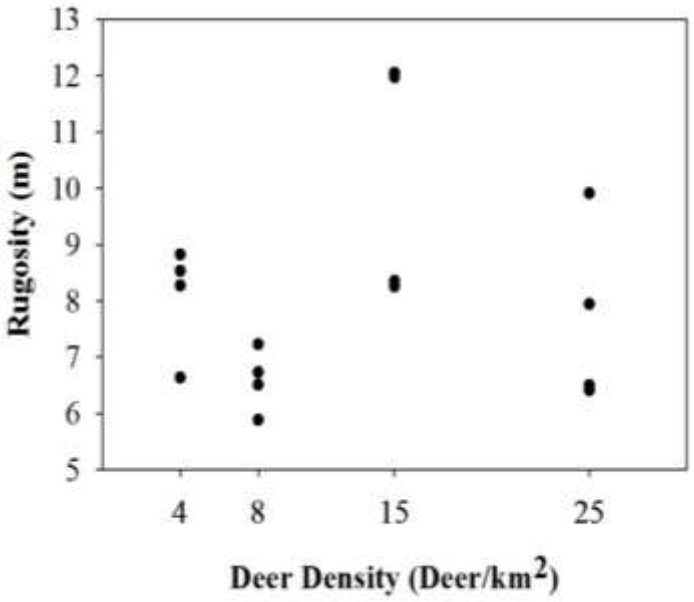

Figure 2: There was no overall trend in rugosity with increasing deer density, but there was a significant increase in rugosity from 8 to 15 deer/km^2 ($p < 0.05$).

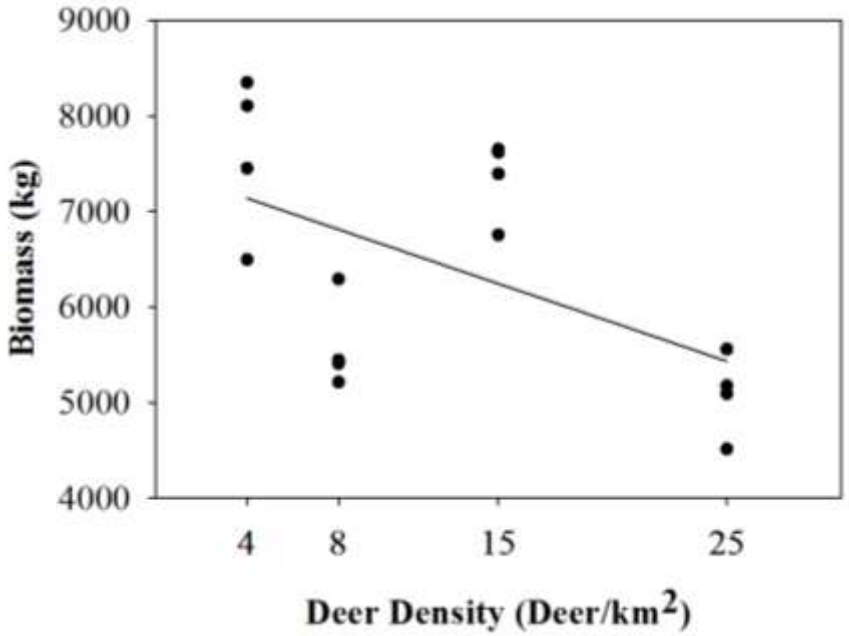

Figure 3: There was a strong negative correlation between deer density and biomass across the plots ($r^2 = 0.244$; $p<0.0001$). The 25 deer/km^2 treatment caused the most dramatic decrease in biomass.

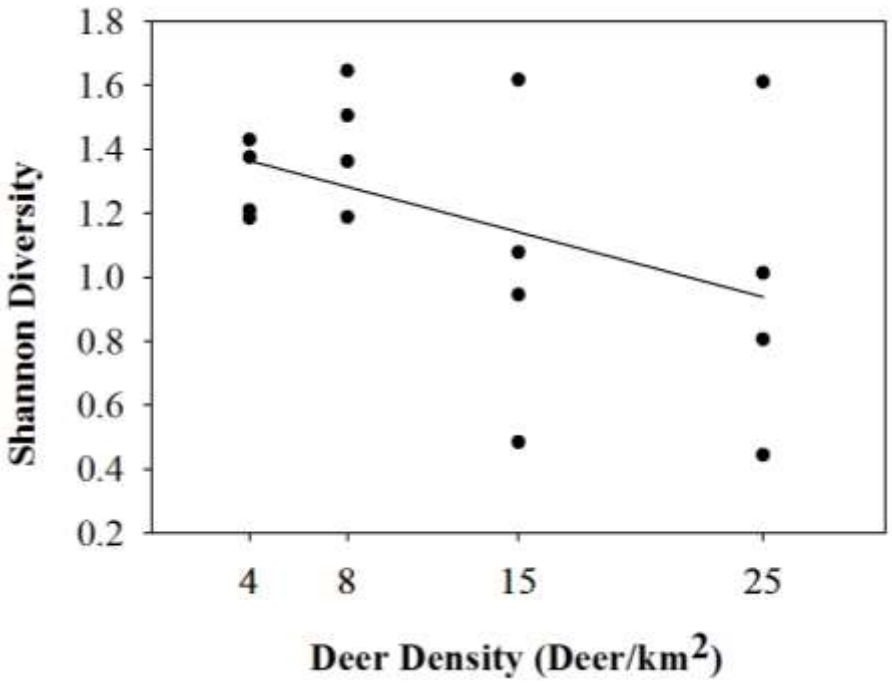

Figure 4: There was a moderately strong negative correlation between deer density and Shannon Diversity ($r^2 = 0.199$; $p < 0.0001$). High variation within the 15 and 25 deer/km^2 treatments could weaken this trend, but may indicate that intense herbivory leads to multiple levels of species diversity and evenness.

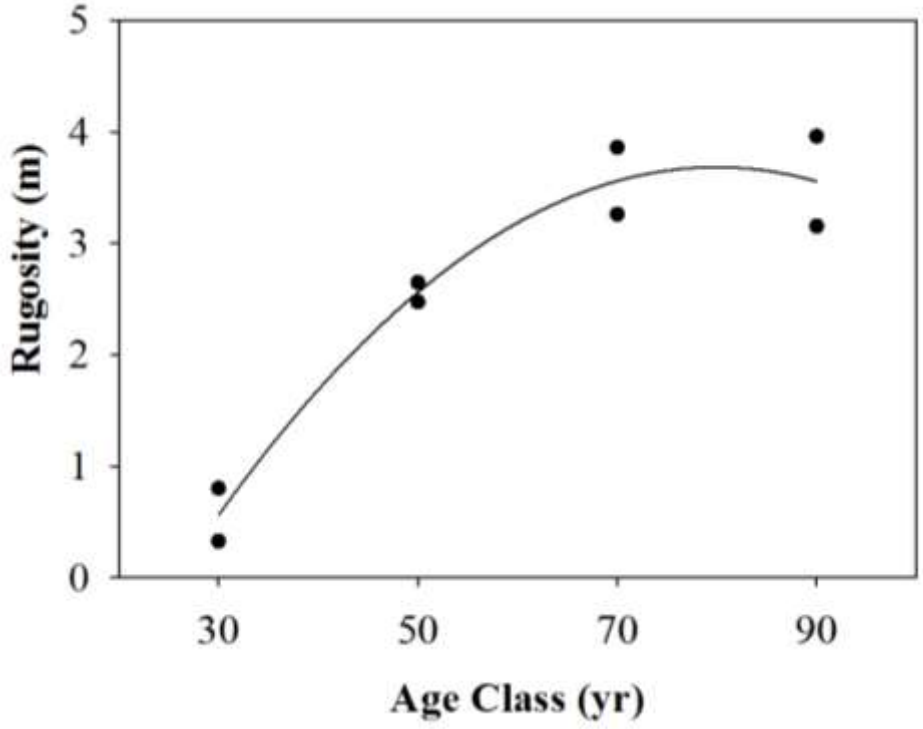

Figure 5: There was a strong positive correlation between white spruce age class and stand rugosity using a quadratic equation ($r^2 = 0.791$; $p < 0.0031$), where the rugosity plateaus at the 70 year age class

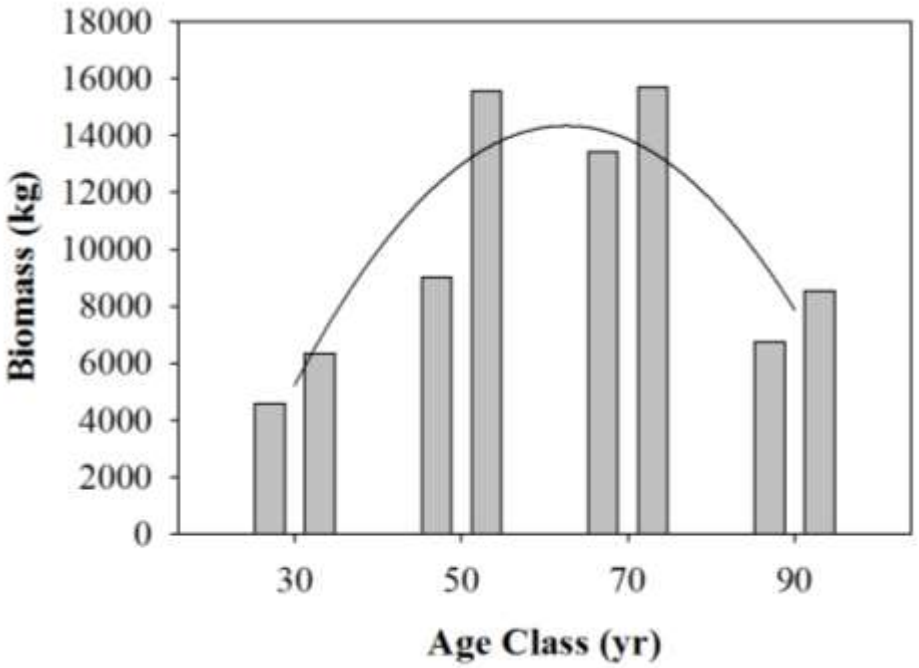

Figure 6: White spruce biomass peaked at the 70 year age class and rapidly fell in the 90 year old stands, creating a parabolic trend ($r^2 = 0.777$; $p < 0.05$)

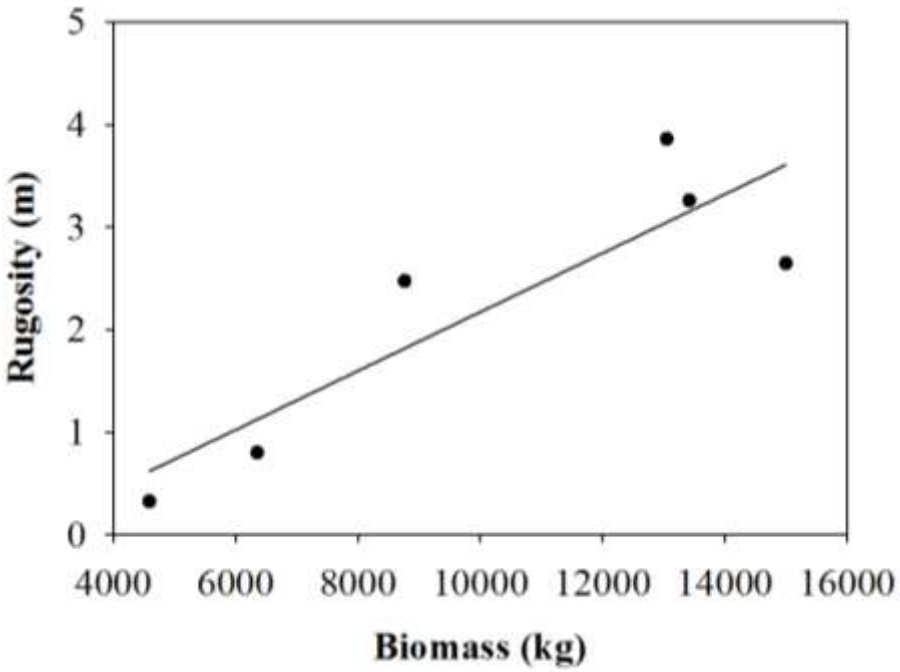

Figure 7: White spruce biomass and rugosity were strongly and positively correlated within the 30, 70, and 90 year age classes. The 90 year age class was excluded due to a decrease in biomass and a plateau in rugosity.

Appendix:

	Rugosity	Height	Mode	ModeEl	Height	MeanStd	LAI	Topel_CPAll	Top_rug	Porosity
DMC1	6.64	4.28	4.36	8.31	6.91	8.44	7.64	11.44	4.33	0.57
WWT1	8.54	4.59	4.10	11.84	9.71	11.73	7.45	14.06	3.28	0.49
GL1	8.83	3.91	3.46	12.16	9.83	11.11	7.53	14.54	2.53	0.45
FC1	8.27	4.95	5.08	10.17	8.11	9.41	7.51	12.48	4.80	0.57
DMC2	6.51	4.24	4.39	9.12	7.52	6.88	6.92	11.26	4.28	0.55
WWT2	7.23	3.50	3.55	7.94	6.15	7.77	7.37	10.31	3.74	0.53
GL2	5.89	4.12	3.96	9.13	7.46	8.24	7.51	12.03	3.65	0.48
FC2	6.73	4.54	4.31	11.03	9.07	9.96	7.52	13.32	3.70	0.50
DMC3	12.05	5.21	5.43	10.04	7.88	12.40	7.84	12.66	5.10	0.56
WWT3	8.26	3.70	3.57	7.03	5.67	6.91	7.41	9.47	4.60	0.57
GL3	11.98	5.26	4.93	13.32	11.18	16.50	7.67	16.51	3.08	0.49
FC3	8.35	4.77	4.72	11.20	9.50	9.17	7.59	13.23	3.96	0.53
DMC4	6.50	4.06	3.95	9.32	7.64	8.18	7.30	11.51	3.27	0.52
WWT4	6.41	3.66	2.65	17.56	15.78	7.32	5.16	18.73	2.09	0.51
GL4	7.94	4.33	3.82	11.90	9.88	9.72	6.18	14.12	3.19	0.52
FC4	9.92	5.71	5.03	13.57	11.50	11.82	5.30	15.29	4.02	0.50

Table A: Aggregation of canopy structural complexity values across deer density treatments